VIII. *The Anatomy and Development of certain* Chalcididæ *and* Ichneumonidæ, *compared with their special Œconomy and Instincts; with Descriptions of a new Genus and Species of Bee-Parasites. By* GEORGE NEWPORT, *Esq., F.R.S., F.L.S. &c.*

Read March 20, 1849.

Preliminary observations.

THE parasitic *Hymenoptera* include, in their larva state, some of the most imperfectly organized conditions of life to be found in the whole of the *Articulata*. They leave the ovum delicate, apodal, almost motionless, and entirely incapable of locomotion, and are injured and perish by slight accident, as an abrasion of surface allows the fluids of their bodies to escape quickly and fatally by the wound; and yet these very beings, having passed unhurt through this scarcely other than fœtal condition, acquire a perfection of organization, a degree of activity and power, and an acuteness of instinct, fully equal, and perhaps superior to the organic and the functional endowments of other tribes of insects. One section of them,—some of which I shall make the subjects of this paper,—are nourished entirely by suction, and subsist on the fluids of other insects; and either attached singly to the external surface of the bodies of their victims, or, located internally, between the tissues, they drink up the life-blood prepared for another, without entirely destroying the means of its production. Other species are gregarious and reside in the same cell with their victim; and while that subsists on vegetable food,—pollen mixed with honey and stored up for it by its parent,—it is attacked on all sides by its insidious enemies, succumbs, and dies as they become nourished. Yet the general form of body, and of the digestive organs, at the earlier periods of growth, is almost precisely the same in most of these descriptions of parasite, and the special development of each is regulated by the same laws. They cast their skin at succeeding stages of growth as certainly as do the larvæ of *Lepidoptera*; but the thrown-off covering is of such extreme tenuity, and is so gradually and almost imperceptibly removed, without interfering with the form or the enlargement of the body, that, hitherto, the deciduation of the tegument of the apodal larvæ of *Hymenoptera* has always escaped the observation of naturalists. I have, however, witnessed its repeated occurrence in the genus *Paniscus*, as I shall show in this paper; so that these species do not constitute, as was supposed, an exception in this respect to one general law. Much as they resemble each other in external appearance, they do so still more in the structure of their organs of nutrition. The digestive apparatus in the whole of them is at first but a simple, capacious sac or bag, rounded and closed at its larger extremity, with an imperforated intestine proceeding from it, without an anal outlet. It has this form in most of these insects during the earlier periods of the larva state, when the organizing

powers of the system are most energetic, and when nearly the whole of the food is appropriated to the enlargement of the body. Very little undigested substance then remains, after the assimilation of the nourishment imbibed, and consequently no excretory outlet to the organ is required. But when the assimilation of food begins to be arrested, and the rapidity of growth is diminished, as is the case when the larva is approaching its maturity,—changes which seem to lead to the inference, that the forces of combination in the primary organisms of the body become less and less energetic in proportion to the degree of stimulus to which they are submitted,—the digestive apparatus then assumes a new form: it is narrowed and elongated, and being connected with a column of granulated cell-masses, which, derived originally from the yolk, are continuous with those that constitute the walls of the digestive cavity at one end, and at the other with the tegument, the cæcal extremity of the sac becomes perforated, and the cells separating in the axis of the column form a tube, that is quickly lined with epithelial membrane, to allow the passage of the refuse of digestion, the tegument having previously separated also at a given point, by which an excretory or anal outlet to the canal is completed. The material first removed is composed chiefly of disintegrated epithelial cells, which line the digestive cavity, and are thrown off as they become aged and worn-out, during the elaboration of nutrient fluid, like the cells which form the cast layers of tegument. This change of structure does not take place in any of the parasitic larvæ, so far as I am aware, until the individual is replete with nourishment, and ceases to feed, preparatory to more extensive alterations of form. When this marked period of its existence has arrived, it is first necessary that the unassimilated portions of food, together with the worn-out materials of the body, should be removed, and this necessitates the change from a closed receptacle to a canal. But further reason for this late completion of the organ, as well in those larvæ which are confined to a given space with their food, and in those still more confined between the tissues of other insects, at once suggests itself. In the one case the food stored up must remain pure and uncontaminated, for the support of the larva preyed upon; in the other, the fluids of the victim must not be changed from nutrient to noxious aliment by the engenderment of disease within it, through contact with effete matter from the body of the parasite, and thus destroy what otherwise it would nourish. But the primary object, the healthy maturity of the larva, being attained, the development of the canal is then completed.

PART I. CHALCIDIDÆ.

The two species I am about to describe are parasites in the nests of the wild-bee, *Anthophora retusa*. They seem to differ in their particular economy as in generic character.

The first species is generically distinct, so far as I am able to ascertain, from any hitherto described genus; the other is a species of *Monodontomerus*, which may prove to be identical with a known species, but of which there is some doubt; so that the name which I propose for it must be regarded as provisional.

Fam. CHALCIDIDÆ.

Gen. ANTHOPHORABIA, Newp.

CHAR. GEN.* *Fem.* *Caput* thorace latius. *Antennæ* 6-articulatæ (?), pilosæ; articulis 2do 3tio 4to 5toque subæqualibus, 6to clavam elongato-ovalem efformante. *Thoraxque abdomen* longitudine æquales. *Alæ* venâ medianâ bifidâ. *Tarsi* 5-articulati.

Mas. *Antennæ* 4-articulatæ; articulo basali arcuato, magnoperè dilatato, infernè excavato; 2do cylindrico, 3tio magno globoso, 4to elongato-ovali. *Oculi* stemmatosi. *Alæ* abbreviatæ.

As the females of this species are the most numerous, and are most likely to be met with, I have regarded this sex as affording good generic characters, although those of the male are the most extraordinary. The name I propose for the species is

ANTHOPHORABIA RETUSA; *Fem.* (TAB. VIII. fig. 2.) Æneo-viridis, capite magno, oculis compositis nigris, abdomine nitido ovali, alis magnis rotundatis, pedibus flavescentibus. *Mas.* (fig. 1.) Flavus vel saturatè ferrugineus, capite magno rotundato ocello utrinque unico tribusque in vertice instructo nigrescente, pedibus robustis.—Long. lin. 1.

Hab. in cellulis *Anthophoræ retusæ*, apud Rutupium in Comitatu Cantio.

In the month of August 1831, while examining the dry clay bank beneath the ruins of the Roman castle at Richborough, near Sandwich in Kent, in search of the larvæ of *Meloë* in the cells of *Anthophora retusa*, with which the bank was thickly perforated, I found many cells filled with an abundance of minute parasitic larvæ, about one line in length, and apparently full-grown; but scarcely a cell contained any vestige of its original inhabitant, the larva of *Anthophora*. During that autumn and the following spring I met with these parasites so frequently in the cells, in different stages of development, that although I regarded them at that time as a new species of *Chalcididæ*, I took little heed of them, as my chief object then was to obtain the Meloës, and as I expected to find them on future occasions in equal abundance. Indeed they were so common as to occasion me considerable annoyance in finding the cells filled with these intruders instead of the larvæ of *Anthophora* or *Meloë*. I took care, however, to make very precise drawings of both sexes, in the perfect state, and of the larva, and also entered some notes of description. In the following years, 1832 and 1834, I again met with them, more especially on the 21st of August in the latter year, but not in such profusion as at first; but I have not been able to procure them since that period.

The *larva* (fig. 3) is completely apodal, of a subcylindrical form, a little attenuated at each extremity, and composed of fourteen segments. The head is small, like that of the wasp, or hornet, and the mandibles are short and acute. It occurred in the bee-cells to the number of thirty or fifty in each. I found it not only in the autumn, but also in the winter and early spring, in this state, but in some cells the larvæ had changed to nymphs before the month of September.

* These generic characters were published in full, together with short specific characters, in the 'Gardeners' Chronicle,' March 24, 1849, No. 12. page 183, in the report of the reading of the first part of this paper.

When the *nymph* (fig. 6) state was attained, at the end of August, the change to the imago occurred in about ten or twelve days afterwards, and the perfect insect hybernated during the following seven or eight months. In most instances, however, no change took place until the spring, the period of hybernation being passed in the state of larva. The fact of the larvæ being full-grown at the end of August, and the cell otherwise entirely empty, seems to indicate that the species is carnivorous and feeds on the young of the Bee.

The *imago*.—The two sexes of this insect differ much in their anatomy and general appearance, and the dissimilarity is so great, that if they were found in separate cells, instead of being constantly together, they might readily be taken for distinct species. The males are heavy and creeping in their movements, scarcely ever making use of their wings, or attempting to escape, but the females are lively and very active.

Description of the species.—The *male* (fig. 1) is of a deep yellow colour, very different from the female, which is of a shining bronze-green. It has a large rounded head, somewhat wider than the thorax, with a single ocellus on each side, instead of the usual large compound eyes of the tribe, and it has also a transverse row of three ocelli on the vertex. The antennæ (fig. 1 *a* & *b*), as I have shown, differ so much from these organs in the other sex, that they might easily be mistaken for those even of an entirely different genus. The prothorax is conical, and the head is supported on it as on a pivot. The mesothorax is somewhat quadrangular, and the scutellum very large. The abdomen in both sexes has seven distinct segments: it is sessile and of a suboval form. The legs are more robust in the male than in the other sex, the tibia and femur being well developed, and the tarsi are five-jointed. The wings are small, narrow, and extend backwards, when folded, as they usually are, to about one half the length of the abdomen. I never have seen the male unfold, or attempt to use them.

The *female* (fig. 2) is of a shining bronze-green colour, with a large head, and large compound eyes at the sides. The antennæ (fig. 2 *a*), as in most of the tribe, are each formed of a long basilar joint, about one half the length of the entire organ, the remaining portion composed of five joints being somewhat elavate. The prothorax and mesothorax resemble those of the male, as also does the abdomen, excepting that it is highly polished. The ovipositor is concealed. The wings are large, rounded, and iridescent, and the insect is exceedingly active on them. The legs (fig. 5 *d*) in this sex are yellow, and less developed than in the male. The number of females in each nest was as six or eight to one of the other sex, the number of the whole in each nest being from thirty to fifty.

I have been unable to find any description in the works of entomologists of this curious genus of parasites. Mr. Walker, our most assiduous monographer of the *Chalcididæ*, is unacquainted with it; and the only naturalist, so far as I can ascertain, who has made reference to an insect which possibly may have some affinity with this, is Mr. Westwood, who, in his work* published in 1839, mentions a species found by M. Audouin in France, in the nests of "*Odynerus*, *Anthophora* and *Osmia*," but he adds that "the species has not yet been described." Since then he has again alluded to M. Audouin's insect †, as

* Introduction to Modern Classification of Insects, vol. ii. part xi. p. 160. (March 1839.)

† Proc. Entom. Soc. Lond., July 5, 1847, p. xviii, in the Transactions, vol. v. part 3. 1848.

having "singularly distorted antennæ, and the wings almost rudimental," thus offering, he says, "a strikingly opposite analogy to other bee-parasites." But without describing M. Audouin's insect, either generically or specifically, or explaining in what its "strikingly opposite analogy" consists, this naturalist has proposed to designate that insect *Melittobia Audouinii*. A name thus given without a description, either generic or specific, cannot, however, be adopted; even if that insect should ultimately prove to be identical with mine. The necessity for precise description when a name is imposed will at once be perceived, in the fact that both Reaumur and DeGeer long ago found *Chalcididous* parasites in the nests of *mason-bees*, and yet, up to the present time, their species have not been clearly made out. Reaumur * found more than thirty larvæ of one species, and in other nests ten or twelve of a larger species. DeGeer † also found twenty specimens of another kind in a single cell, and which he reared to the perfect state. He remarks, too, that the larvæ of mason-bees are very subject to be destroyed in their cells by the larvæ of different species of *Ichneumon*. The species found by DeGeer seems to have been a *Pteromalus*, or nearly allied to that genus. These facts are interesting, as showing that mason-bees are infested by many parasites. The occurrence of Audouin's insect in the nest of *Odynerus*, as well as of *Osmia* and *Anthophora*, as stated, renders its identification with the insect I have discovered very doubtful. I have never found my species in any other than the nests of *Anthophora*.

The *habits* of this insect may be inferred from the peculiar organization of the male. From both sexes being found in the closed cells of the bee, and from the absence of a long ovipositor in the female, we may conclude that the eggs are deposited while the nest is being provisioned, or immediately before it is closed; and that, like the true *Ichneumons*, the parent either plunges her eggs into the body of the newly-hatched bee-larva, or attaches them to its skin. The bee-larva, like many other species similarly circumstanced, continues to feed, and grow, and supply nourishment to the parasites; and by the time it has consumed the whole of its provision, these also are far advanced in growth. When the young bee is entirely destroyed these are matured, and prepare for their change to the state of nymph, which they assume lying loosely in the cell, without spinning separate cocoons.

From the circumstance that although both sexes are found moving about freely in the cell, the male is by far the least active, and especially from the fact that his organs of vision are merely single ocelli, instead of large compound eyes, as in the other sex, I am led to the conclusion that impregnation is effected before the insects quit their habitation; because ocelli, being different in their structure from the individual parts of the compound eyes, are fitted only for near vision. The difference of structure consists in this: the cornea, or external surface of each part of the compound eye, which is individually as perfect, as an organ of vision, as the ocellus, or single eye, is less convex than the cornea of the latter; while the *chamber* of the eye, or space between the cornea and the termination of the nerve at the bottom of the structure, is of much greater length in the com-

* Mémoires pour servir à l'Histoire des Insectes, tome vi. part. i. p. 98. 12mo. Amsterdam, 1748.

† Mémoires, tome ii. part. 2. p. 887–8. pl. 30. fig. 23–25.

pound eye than in the single. The result of these two conditions is, that the compound eye is fitted for viewing objects at a considerable distance, but with little magnifying power; while the ocellus has great magnifying power, but is fitted only for viewing near objects. The male with his single eyes may thus be regarded as acute, but *short-sighted*, the very opposite of his partner. But this condition is essential to him, and fully sufficient, if, as presumed, the greater portion of his existence is passed in a closed cell, not half an inch in diameter, and from which perhaps he never wanders more than to the distance of a few inches. But stemmata or ocelli only would be insufficient for the other sex, who has not only to seek out the proper locality for her eggs, but also to elude the vigilance of the bee in whose nest she is seeking to introduce her own progeny. Instead, therefore, of mere stemmata, the eyes of the female are multiplied, and occupy, as in most other perfect insects, a large portion of the surface on each side of the head. Each of these aggregated eyes has a much greater length of sight, or distance of vision, than is afforded by the different structure of stemmata; while the multiplicity of these organs at one spot supplies to the insect at once long focal distance, or long-sightedness; and their multiplicity more than compensates for the narrowness of the field of each cornea.

The conclusions, then, which are deducible from the structure of the organs of vision seem to be, that whenever an insect is provided only with stemmata, the habits of the species, in that state of existence, are restricted to a few objects or requirements; or that the species is limited in perception and locality; while, on the contrary, when the organs of vision are multiplied and aggregated to form what we designate a *compound* eye, as in the imago state of most perfect insects, the field of vision, as well as the focal distance, or length of sight, and with these the range of the insect, are greatly extended.

Other facts in the comparative anatomy of this parasite confirm these conclusions. The short closed wings of the male, as noticed by Mr. Westwood in regard to the undescribed insect *Mellitobia* *, contrasted with the wings of the female, lead us to infer that the former sex rarely or never employs them in flight, and confirm the opinion that impregnation is the sole requirement for the male, and is effected within the cell.

This condition of the sexes affords a remarkable contrast to that of *Stylops*, which I formerly had the honour of bringing before the notice of this Society, Jan. 19, 1847†. In that genus, as will be remembered, the worm-like female is sought out by the active male, in which the organs of vision, as in the equally active males of the Hive-bee and Glow-worm, are enormously multiplied, yet merely for one single act of existence—the continuation of the species.

Thus it may be seen that under every form of body, and of each individual organ, the special anatomy of a species is an index to its natural history and economy.

The second Chalcididous parasite, which I have found in the nest of *Anthophora*, is an insect of different character from the one just described, but equally illustrates the general views now proposed.

* Compare Mr. Westwood's remark on M. Audouin's insect above referred to, Introduction, &c., vol. ii. p. 160.

† Linn. Trans. vol. xx. p. 347–349.

Monodontomerus nitidus.

On the 12th of September, 1847, I detected, in several cells of *Anthophora retusa*, in a dry clay-bank at Gravesend, a number of white Hymenopterous larvæ, which at first I mistook for those just described. There were from twelve to twenty-five in each cell, apparently full-grown, and measuring each about one quarter of an inch in length. The body, in these larvæ (fig. 7 & 8), was formed of fourteen distinct segments, each divided transversely on the dorsal surface into two, and covered with exceedingly fine, scattered, brownish hairs. The head was small, and provided, as in all parasitic *Hymenoptera*, with short, transverse, corneous mandibles, and the larvæ had considerable power of locomotion, by the extension and shortening of the segments. The whole of the food that had been provided for the bee-larva was already consumed, and the bee-cell contained only the parasites and the dried tegument and head of the young bee, which seemed to have been starved. It was a question with me whether the bee-larva had not been killed by the other larvæ piercing it, and abstracting its fluids from without? This query, then, seemed to be answered by the circumstance that the number of the parasites was disproportioned to the size of the victim, which, had it served as food for them, would in all probability have been entirely consumed. Besides which, one anatomical fact showed that they were external feeders,—their bodies were covered with a few scattered hairs, appreciators of contact; a condition which I have never yet observed in the soft-bodied, internal-feeding larvæ of other *Hymenoptera*, and one which is as little required by them, as it doubtless would be inconvenient. Added to this, the great power of locomotion possessed by these larvæ,—which is neither possessed nor required by internal feeders, which remain almost constantly in the same spot,—suggested the opinion that it is on the food of the bee that these larvæ subsist, and not on the young bee itself, which may perish merely by deprivation of its proper nourishment. The larvæ also exhibited some indications of the formation of an anal outlet to the alimentary canal, which are not apparent in internal feeders at this stage of growth.

I preserved these larvæ, in the cells in which they were found, through the following winter, and although the remains of the bee were left with them in the cell, it continued untouched, and they exhibited no further change until the middle of May 1848. At that time some of the specimens gave signs of approaching transformation, in the shortened and more shrivelled appearance of their bodies. Each of the larvæ then spun some very delicate silk, in small quantity. Shortly before they were ready to enter the nymph state, the alimentary organs became perforated, and fæces were then passed for the first time during the whole period of the insect's previous existence. The fæces passed were little solid brown masses, that closely resembled the fæcal masses passed by the pollinivorous larva of *Anthophora*, which, like its parasites, as I have constantly found, passes nothing from its alimentary canal until it is about to change to a nymph. These fæcal masses seemed to indicate the supposed nature of the food,—pollen and honey; and to support the opinion formed of the habits of these larvæ from some points in their external anatomy. From twelve to twenty masses were passed by each larva: these were composed of the refuse of digestion and of epithelial cells accumulated during the period of feeding, and

retained in the digestive sac until the period of its perforation. In this way the food and abode of the insects are maintained pure and uncontaminated, and the digestive apparatus is completed, and the refuse of nutrition ejected only when the whole of the food has been consumed. Thus we find the most perfect concordance between the internal as well as external anatomy, and the functions and economy of the animal, exemplifying in every particular the harmony of creation.

I have stated that the digestive cavity is at first a closed sac. This species has enabled me to demonstrate the fact, and further to illustrate the manner in which it is changed from this form to that of a tube or canal.

On dissecting this larva, I found that nearly the whole interior is occupied by the digestive apparatus, which has the form of a bag, or rather of a Florence flask (fig. 9). Proceeding from the mouth and pharynx is a narrow short œsophagus (*a*), which suddenly enlarges into the common cavity (*b*): this occupies nearly the whole of the interior, and has extremely thick walls, formed of large packets of granulated cell-masses, inclosed between an exceedingly delicate muscular envelope on the external surface, and an equally fine, granulated membrane on the internal. It is divided from the œsophagus internally by a thick fold of its mucous and celliform tissues, which here constitute a complete cardiac valve (*c*), and prevent the regurgitation of the food. At the posterior, or larger end (*d*), it is connected with a column of cell-masses (*d d*), which have partially coalesced on the exterior, in the formation of a fibro-cellular envelope, and which, proceeding backwards, are united with the common tegument of the body in the fourteenth, or anal segment (*f*). In the centre of this segment, on the external surface, the skin and muscles separate at a definite point in the formation of the anal outlet. When the change is about to commence, the cell-masses that form the cæcal end (*g*) of the cavity also separate and recede, and this separation extends backwards to the fourteenth segment in the axis of the column of cells. By the centrifugal expansion of these, and the consequent widening of the tube, the canal is completed, and quickly becomes lined with a delicate membrane, like the interior of the larger cavity. The digestive organ is enveloped in a thick layer of granulous matter, in which the Malpighian vessels (*h*) and the organs of reproduction are developed. At its anterior and inferior surface it covers two large sacs, the silk-glands (*i*). These are the first developed organs of this class of structure, and are needed thus early for the production of the silk which the larva spins before its change.

The *nymph state* (fig. 11) was assumed by two of my specimens at the end of May. On the 30th of that month I found that three others also had undergone their change, and that the remaining ones were preparing to do so. The nymph had the usual form of the tribe, and the sexes were now for the first time distinguished. The male nymph was smaller, more slender, and with the apex of the body acute; while the female was much larger than the male, with a short projecting keel at the posterior of the abdomen—the ovipositor.

The *imago* (fig. 12).—On the 27th of June, about four weeks after entering the nymph state, one of the female specimens threw off its envelope and became perfect, and proved to be a species of the genus *Monodontomerus*. A few days afterwards one of the males appeared; and in the course of a week, before the 3rd of July, most of my specimens had become perfect.

Of fifteen specimens allowed to complete their changes, there were only two males, with thirteen females. The remaining specimens I had preserved in their larva and nymph states for dissection. This small number of males coincides with the small number of this sex in other bee-parasites; but the deficiency in numbers is fully compensated for by the activity of the individuals.

The fewness of the males, and their great activity, lead me to believe that the females are impregnated, not *before*, but shortly after they have left the cell, and in the hot sunshine. Like the *Chrysididæ*, these insects are active only in strong light. Both sexes of my specimens always became dull and motionless when removed from the light; but when exposed to the sun they immediately resumed their activity. They seem to live but a short period in the imago state. The males died within a few days, and the females in about a fortnight.

I have proposed for this species the name of *nitidus* *, from its elegant and glistening appearance. It may be described as follows:

MONODONTOMERUS NITIDUS.

Male.—Head and thorax brilliant shagreen, with fine short hairs: head broader than the thorax, face bluish; labrum emarginated; eyes and ocelli large, dark brown; antennæ 11-jointed, basal joint coppery. Prothorax compressed and slightly excavated at the sides. Metathorax and scutellum large. Abdomen green bronze, hairy, petiolated, very much compressed at its base, and keeled on the ventral surface; first and second pairs of thighs green; third pair large, copper-coloured; tibiæ and tarsi fuscous, very hairy. Wings hyaline, hairy, with black costal spot. Length two lines and a half.

Female (fig. 12).—Head and thorax brilliant shagreen, hairy: head large; face blue, punctured; eyes and ocelli large, brown; antennæ pubescent, 11-jointed, with the basal joint coppery, as in the male. Thorax compressed laterally. Scutellum very large. Thighs green, shining. Tibiæ and tarsi hairy, fuscous, with an acute spine at the articulation of the tibiæ. Abdomen coppery, polished, with a few white hairs, subsessile, compressed at its sides, and strongly keeled; ovipositor exserted, longer than the abdomen, and very acute. Wings dusky iridescent, hairy, and with dark marginal spot. Length of body two lines †.

From the length of the ovipositor in this insect, we may conclude that the female does not enter the bees' nest to deposit her eggs; but that she perforates the cell and conveys them into it, after the cell is closed, and probably after the young bee is hatched. Every part of the anatomy of this insect, as of the preceding, and of every other species when attentively considered, will thus be found to exemplify its general economy, and to indicate how closely the one is connected with the other,—how intimately associated is the instinct of a living being with special conformations of its organism. Some other families of Hymenopterous parasites are marked instances of the unfolding of peculiar instincts subsequent to the development of particular structures. Amongst these we may notice two of the true *Ichneumonidæ*, *Paniscus virgatus* and *Ichneumon Atropos*.

* This name was proposed for the insect at a Meeting of the Entomological Society, on the 3rd of July, 1848, and the discovery of the larva in the nests of *Anthophora retusa* was then mentioned. See Proceedings, Ent. Soc. Trans. vol. v. part 5. p. xlii. 1848.

† Mr. Walker has recently re-described this species as "*Monodontomerus Anthophoræ*, Newp." See Ann. and Mag. of Nat. Hist. vol. ix. No. 49. Jan. 1852, p. 43.

Postscript to the foregoing Section of this Paper.

Read May 1, 1849.

I am desirous of appending a few remarks to the section of this paper that has already been communicated to the Society, before proceeding with the remainder.

These refer to the second bee-parasite described, and provisionally named *Monodontomerus nitidus*. The parasitism of insects of this genus on *Anthophora* had not previously been ascertained. *M. obsoletus* had been suspected of infesting the genus *Osmia**, like one of its affinities †, but its larva, so far as I am aware, was unknown. I found the larva of *M. nitidus* in the nests of *Anthophora*, on the 27th of September, 1847, and mentioned the fact to an entomologist, Mr. F. Smith, who, some time afterwards, as he himself informed me, obtained specimens of it from the same locality. From a note on its habits, which he has recently communicated to this Society ‡, it appears that the larva is carnivorous, and feeds on the bee-larva, and not on its food, as I had believed. I am thankful for this correction of observation. The mistake arose in my haste to furnish part of this paper for reading to the Society by a given time, which obliged me to forego an examination of the parts of the mouth, which are difficult to observe, and compelled me to rely on the appearance of the fæces, and on the fact of having found my full-grown specimens in the cell of the bee with the dried-up remains of the bee-larva. I have now made the required observations on the oral organs, and also have microscopically examined the contents of the digestive apparatus, and these lead me to agree with Mr. Smith in regarding the larva as carnivorous, and not as pollinivorous. The mandibles are slender, arched and acute, and are fitted only for piercing, and not for comminuting food; the labium and maxillæ are thick, large and membranous, somewhat like those of the larva of *Paniscus*. The contents of the digestive apparatus I found to consist of large and small nucleated cells, consolidated together, and darkened in appearance, conditions induced probably by admixture with secretions from the parietes of the apparatus during digestion.

Thus further examination of this larva tends but to confirm, instead of to confute the general view which I have constantly maintained,—that structure, when carefully and accurately investigated, is an infallible index to function and habit. My incorrectness in opinion as to the particular kind of food of the larva of *Monodontomerus* was the result of hurried and incomplete inquiry, and it is now rectified by direct observation on the habits of the insect, and by closer attention to its anatomy. Yet the main object of this paper was but little affected by the error, my aim being to show not merely that Hymenopterous parasites may differ in their kind of food, but the more general fact of a concordance between structure and kind of life;—and also that whether the Hymenopterous parasite is shut up in the same cell with an insect that continues to feed, or whether it preys on the surface or interior of such insect, its alimentary canal is closed and incomplete until it has ceased to take food and has acquired its full size, when the canal becomes perforated, and allows a passage for the ejection of the refuse of nutrition; the necessity for this late completion of the organs of digestion having reference to the preservation of the food of the parasite in a condition fitted for its proper nourishment.

* Westwood's Introduction, &c., vol. ii. p. 160. † *Id.* ‡ Proceedings, vol. ii. p. 29.

PART II. ICHNEUMONIDÆ.

Read May 1, 1849.

Paniscus virgatus, Foure.

The parasites of the genus *Paniscus*, and their affinities *Ophion*, which are some of the most active and percipient of insects in their perfect state, are examples of one of the very lowest forms of life as larvæ, as well as of one of the most curious modes of nutrition. In the earlier stages of growth they more resemble cotyledonous vegetables, in general appearance, than animal organisms which are destined to become some of the most perfect, and most active of their Class. I have traced *Paniscus virgatus* from the bursting of its egg to its assumption of the imago state, and have watched its growth and the formation of its tissues.

The earliest notice I am acquainted with on the habits of an insect of this family is of *Ophion luteum*, by Gœdart *, who found five specimens of the imago produced on the 29th of June from the hard cocoon formed in September of the previous year, by the larva of *Cerura vinula*, L. Bonnet † afterwards, as quoted by DeGeer ‡, made some observations on the singular economy of this insect. He remarked that the eggs of *Ophion* are attached to the outside of the body of the caterpillar of the Puss-moth, by a short pedicle or footstalk inserted into the skin, and that the parasite when hatched is nourished on the outside of the body, still attached to its shell and pedicle like a vegetable growth. DeGeer § found the same insect on the Puss-moth larva, and ascertained that several individuals subsist on the same caterpillar, which dies of exhaustion after it has formed its hard wooden cocoon. More recently the eggs of this genus have been the subjects of a memoir by Dr. Hartig, as mentioned by Mr. Westwood ‖, but this memoir I have not yet seen. I do not pretend, therefore, to claim entire originality for the few observations which I have made on *Paniscus*, but merely to state what I have myself observed, in accordance with the views I have proposed.

On the 26th of September, 1847, I found many nearly full-grown larvæ of the Broom-moth, *Mamestra pisi* (fig. 13), feeding on that plant in the hot sunshine. On the following day I detected a number of little shining black-looking bodies (*a*) on one of these larvæ, attached to different parts of its three thoracic segments. On examining these bodies more closely, I found to my surprise that they were black shining eggs (*a*), inserted at one end into the skin of the caterpillar. These eggs were somewhat oval, or rather pear-shaped, the attenuated footstalk being lodged under the skin. There were eight thus attached. But what fixed my attention closely was, that most of the eggs had already burst, or were in the act of bursting longitudinally (14 *c*), precisely as I have formerly seen and described in the eggs of the *Iulidæ* ¶. Each egg had divided in the middle line, at its anterior extremity, and the two halves of the shell were separating like the cotyledons of the seeds of

* Métamorphoses Naturelles, 12mo, tom. ii. p. 162. pl. 37. À la Haye, 1700.

† Mémoires de l'Académie des Sciences de Paris. ‡ Mémoires, tom. ii. p. ii. page 851.

§ *Ibid.* p. 852, 853. ‖ Introduction, &c., vol. ii. p. 146. ¶ Phil. Trans. 1841.

leguminous plants, whilst the head of the little white larva was slowly passing out between them (14 *a* & *b*), like the germ-roots, to become affixed by its mouth to the skin of the caterpillar, the body being retained within the shell. As the parasites became attached, the fated caterpillar moved about with increased rapidity, twisting and turning its body in every direction, and evidently endeavouring to get rid of its new-born enemies, but to no effect. The little beings, securely affixed by their shells, giving no evidence of sensation, and scarcely even of vitality, were unaffected by these endeavours to displace them, and retained firm hold. The cleavage of the shell was chiefly on the under surface, so that the two halves formed a kind of bivalve covering or cloak to the larva, and clasped its body as the head emerged. The head at first was the only portion of the larva that was exposed. But the little creature grew rapidly, deriving its nourishment by slight puncture and suction through the skin of the caterpillar, with scarce an abrasion of the surface. The rapidity of its growth in this way was truly astonishing, the whole of the nutriment thus imbibed being appropriated to its increase, excepting only the very little expended by cutaneous transpiration; for respiration at this early period can scarcely be proved to have commenced, as I was unable at this stage to detect the respiratory organs, while the digestive cavity, as we have already seen in other parasites, was imperforate. Within *two hours* from the bursting of the shell there was a marked increase of size in the larva. In the course of the *first day* the prothorax and the head were extended from the shell, and early in the *second day* the three thoracic segments, as well as a large portion of its ventral surface, were exposed, the larva (fig. 15) then being nearly twice its original size in the ovum. When examined by a lens it seemed to be almost entirely formed of an immense stomach, connected with the mouth by a short and very narrow œsophagus, as in the larva of *Monodontomerus*. The motions of the stomach, vermicular and incessant, were distinctly seen through the tegument. As the insect increased in size, it was more and more extended from the shell. Its anterior part grew the most rapidly, the largest segment being the first, or prothoracic.

It was not until after the completion of the second day that I was able to detect the respiratory organs through the tegument, although I had previously sought for them with much care. The little vegetating being then seemed like an embryo, which,—instead of deriving its means of growth, like other embryos of its class, in the unburst egg by imbibition of fluid from without, through its shell and membranes,—had been prematurely exposed by the sudden rupture of its envelope, and left to perish, or to absorb adventitious nourishment from other bodies. I could not help regarding it among insects as the representative of the embryo Kangaroo among quadrupeds, prematurely liberated from its fœtal coverings, and extruded from the body of its parent, to continue existence attached externally to the teat in the marsupium. But still more closely did it resemble the embryo of the inferior *Myriapoda*,—the *Iulidæ*, in which the young, after bursting its shell longitudinally, as in *Paniscus*, is detained within it, and continues to grow by imbibition of nourishment through its membranes from the surrounding medium. There is, however, this difference. In the *Iulidæ* the retained embryo is inclosed in its membranes after the shell is burst, and does not throw them off until it has acquired organs of locomotion and is able to move about and seek food. But the young *Paniscus* bursts its

membranes with its shell, although it is completely apodal and incapable of locomotion, and has to derive nourishment, not by simple endosmosis through its fœtal envelopes into the tissues of its body by similar means, but by the direct abstraction of fluid from another living body into its own. To ensure this, the larva requires to be attached by its terminal segments to its shell during the whole period of its growth, and like the larvæ already described, it passes no fæces until it has attained its full growth, and becomes detached from its shell, to prepare for its change to a nymph.

After the second day I was accidentally prevented for some time from making any very precise observations on these insects, further than noticing that they grew rapidly from day to day, and that they retained their connexion with the shell.

On the 4th of October, the *ninth day* of their existence, I was enabled to resume my examinations of them, and then found that several of them had perished, and that three only remained healthy and thriving. The caterpillar on which they had fed had become shrunken and wasted, but still retained sufficient irritability and muscular power to contract its body with a quick lateral motion when touched. The larvæ that remained healthy were now at least twelve times their original size (fig. 16). The head (16 *a*) of the larva, which at first was the most ample region of its body, was now the smallest, relatively to other parts which had increased more rapidly, and but little exceeded the size of the ovum. The parasites were attached, one on the dorsal surface and one on each side of the caterpillar, the latter one coiling round the inferior surface of the thoracic segments (fig. 17). Their bodies, enlarged and fattened, were of a dark pea-green colour, and were formed each of fourteen segments, all of which, more especially the anterior ones, were distinctly marked. The stomach in each was in a state of incessant to and fro vermicular motion, and had become enveloped in a thick tissue of little white follicles, which have been regarded as the rudiments of fat-vesicles. No anal outlet had yet been formed, nor was there, so far as I could discover, any perforated intestine. In the interval of seven days, during which I had been prevented from following up my observations, each larva had three times cast its tegument. This, I believe, is the first time that the soft-bodied Hymenopterous larvæ have been noticed to undergo this change. These larvæ, therefore, as I have already pointed out, are not exceptions, as they have been suspected to be, to the general rule of development in hexapods, in so far as refers to the casting of the skin; although, as the body is still connected with the egg-shell, the cast teguments are not entirely got rid of until the larva is detached to become a nymph. The skin is fissured in *Paniscus*, as in other larvæ, along the dorsal surface of the anterior thoracic segments, and is gradually removed from the dorsal, lateral, and inferior surfaces of the head and succeeding segments, by the growth and expansion of the new tegument beneath it, the fissure being extended, and the covering slipped off from above downwards and backwards, as much by the rapidity of growth in the parts beneath, as by the occasional slight muscular contractions of the segments. When I re-examined my specimens on the *ninth day*, neither of the cast layers had been removed further than to the posterior segments of the body, which they partially inclosed. The *first shed* skin (fig. 16 *a*) was attached to the anal segment, and enveloped this part, surrounded by the shell, and covering the inferior surface. The *second* (*b*), within the first, but larger and more corrugated, partially sur-

rounded the twelfth and thirteenth segments: and the *third* (*c*), the deciduation of which I had the good fortune to witness, while examining the larva for other purposes, was internal to, and partly covered by, the second, and was not forced back further on the ventral surface than to the *ninth* segment, although, like the preceding, it was entirely removed from the dorsal surface. The whole thus formed a kind of treble sheathing to the posterior segments of the body, until the period when the larva, full-grown to repletion, was to prepare for its transformation, become detached from its shell, and leave its deciduated coverings in connexion with it. On the *tenth day*, October 5th, the larvæ had further increased in size, were more raised from the body of the caterpillar, and lay coiled up in a more circular form. Each one was still attached to its egg-shell, although now more than twenty times its size, and each adhered to the caterpillar by its oral organs, exhausting and impoverishing it of its juices. The skin of the parasite again appeared tense and dull, as when about to be cast. The head and thorax had a whiter and more fibrous appearance, the stomach was less easily distinguished through the tegument from other viscera, excepting at intervals, and the heart was seen in motion along the dorsal surface, but with little regularity in its contractions. Its movements appeared to be greatly influenced by the motions of the digestive apparatus, which seemed to induce the tissues around it to contract, and thus excite a reflected action in the circulatory organ, the movements of which appeared to be greatest in the middle of its chambers. The tissue which has hitherto usually been regarded as the *adipose*—and which I may hereafter have occasion to notice more particularly—was now much extended and augmented in size, and the respiratory organs, although extremely simple, were become well marked. On the *eleventh day* the larva was still larger, and became detached from the egg-shell; but whether this resulted from accident, or from the completion of its growth, I was not then able to determine. Its tegument had become more opake, and there were tubercular projections at the sides of its abdominal segments, immediately below the line of longitudinal tracheal vessels. On the *twelfth day* I found that the separation of the specimen from its shell was accidental and premature, and that the larva was unable to re-affix its oral organs to the skin of the caterpillar and perished. This is usually the case when a larva is prematurely detached; and this result explains the necessity for the continuance of its connexion with the egg-shell, which, as DeGeer has observed of the eggs of *Ophion*, is so firmly inserted into the caterpillar that it cannot be removed without lacerating the skin.

My further observations were now continued on the other specimens of the same brood, which had been more slow of growth. On the *fifteenth day* one of these was mature, and separated from the shell, leaving its cast teguments forced into a little mass attached to it. DeGeer* formerly noticed that the larva of *Ophion* left something connected with the egg-shell, but he does not appear to have been aware that it was the entire cast skin of the larva. My specimen of *Paniscus* now measured somewhat more than half an inch in length, was of a curved form, and was smallest at each extremity. Mr. Westwood† has already indicated this as the general form of body of the larva of this tribe of parasites, and has mentioned that they have lateral fleshy tubercles. He has described the parts of the mouth as consisting of "two obliquely deflexed horny mandibles, very small, slender,

* Mémoires. † Introduct. vol. ii. p. 147.

and acute, beneath which is a curved fleshy lobe, formed by the union of the dilated maxillæ and labium." In this account he is perfectly correct. But while challenging the description given by Reaumur of the head of the larva, he appears himself to have fallen into the singular error of mistaking the rudiments of the future antennæ for ocelli. He says *, "The head is furnished with two distinct round points—resembling ocelli," but he makes no allusion to the existence of antennæ. No organs of vision exist in any of the parasitic *Hymenoptera* at the "points" he has indicated in his text and figure of the head of these larvæ, the parts referred to being the apices of the antennæ of the future imago. I have traced the antennal nerves into these parts in the larva of *Ichneumon atropos*, which closely resembles in this respect that of *Paniscus*. The small size and deflection of the mandibles partly account for the difficulty which this larva has in re-attaching itself to the caterpillar when detached from its shell, and the consequent necessity for this attachment for its preservation,—premature removal resulting in starvation, as with my first specimen. My second specimen, which left the shell only when matured, I placed on some light mould, in a covered glass vessel, to observe its changes. I expected to have seen it bury itself in the earth, knowing this to be the habit of the larva on which it feeds; but in this I was disappointed. Its instincts were more limited and imperfect than I had imagined. On the day after placing it on the mould, it was lying in a slight hollow on the surface, made by contracting and turning its body, and was in the act of spinning a delicate web of silk, under which it was lying, and where I hoped to have seen it change to a nymph. It attached a few grains of earth to the inside of the web, and between the threads scattered here and there, like the particles of earth interwoven with its threads by the caterpillar of *Mamestra*, but after remaining at rest for a couple of days, I found it discoloured and dead.

Thus checked in my observations, I had no hope of being able to complete this inquiry by tracing the insect to its imago state, until, on the 6th of April, 1848, I found, on examining the earth in a breeding cage, in which I had kept many larvæ of *Mamestra pisi*, to obtain the pupæ of that insect,—in several earthen cocoons formed by the caterpillar, —from two to three cylindrical leather-like cases of a black colour, applied so closely together that their walls formed angular surfaces, precisely like the cells of a honeycomb, or wasp's nest. There were from two to three of these cylindrical cases in each earthen cocoon of *Mamestra*. Each cylinder measured about six-tenths of an inch in length. In some cocoons there were three cylinders, and in one only I found four. In the latter instance they were smaller than when the cocoon contained but two, as if the inmates had not been sufficiently fed. This was markedly the case with two of the four specimens found together, which were scarcely more than one-half the size and length of the others. Each of the cocoons of *Mamestra* was completed in the usual mode of this larva, its earthen walls being smoothed on their interior, agglutinated together, and lined with silk; and each contained, besides the cylinders of the parasitic insects, the dried-up remains of the caterpillar.

From these facts it seems to follow, that the economy of the parasite is this: the parent Ichneumon-fly deposits her eggs on the caterpillar when this is nearly full-grown, and

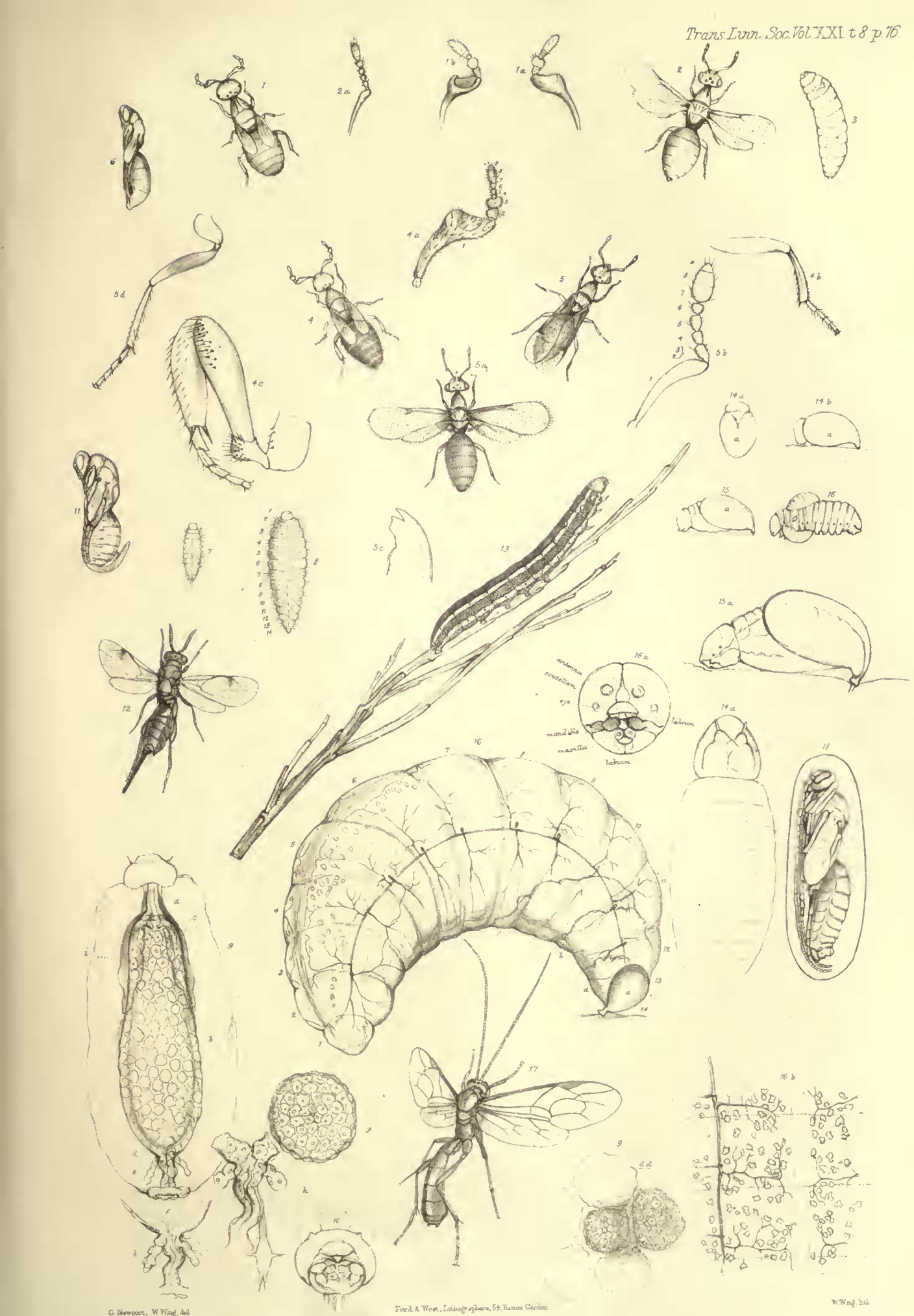
* Introduct. vol. ii. p. 147, fig. 76. 14, p. 140.

will soon enter the earth, which it does, as I presume must have been the case with these insects, while the parasites are very young and small, otherwise they may be injured or detached while the caterpillar is burrowing and making its cell. The fated insect, exhausted by the parasites, has but sufficient strength to complete and tapestry its earthen chamber before it dies, leaving its newly-formed abode to the occupation of its enemies, which grow rapidly, as we have seen, pass through the changes I have traced, and then form their own cocoon in which they are metamorphosed to nymphs.

On examining one or two of the cylinders at the time of obtaining them in the beginning of April, I found that the inmates had very recently changed to nymphs (fig. 18).

On the 8th of May one of these assumed the imago state (fig. 19), but escaped on my incautiously opening the box that inclosed them. On the 14th two more appeared, and I now had the means of identifying the species. It proved to be as I have stated, *Paniscus virgatus*.

It is probable that these insects may have come forth at a period earlier than in their natural haunts, having been kept in a warm room, and the temperature of the season, at the time of their evolution, being considerably higher than usual. It is worthy of remark, however, that the moth, or the larva of which this *Paniscus* is a parasite, kept during its pupa state under precisely similar circumstances, had already made its appearance a week at least previously; so that, under similar conditions of locality and temperature, the parasites came forth at the latest period.



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